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SIMULTANEOUS USE OF MARK–RECAPTURE AND RADIOTELEMETRY TO ESTIMATE SURVIVAL, MOVEMENT, AND CAPTURE RATES

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Abstract: Biologists often estimate separate survival and movement rates from radiotelemetry and mark–recapture data from the same study population. We describe a method for combining these data types in a single model to obtain joint, potentially less biased estimates of survival and movement that use all available data. We furnish an example using wood thrushes (*Hylocichla mustelina*) captured at the Piedmont National Wildlife Refuge in central Georgia in 1996. The model structure allows estimation of survival and capture probabilities, as well as estimation of movements away from and into the study area. In addition, the model structure provides many possibilities for hypothesis testing. Using the combined model structure, we estimated that weekly survival of wood thrushes was 0.989 ± 0.007 (±SE). Survival rates of banded and radiomarked individuals were not different ($\hat{\alpha}[S_{radioed}, S_{banded}] = \log[\hat{S}_{radioed}/\hat{S}_{banded}] = 0.0239$, 95% CI = −0.0196 to 0.0486). Fidelity rates (weekly probability of remaining in a stratum) did not differ between geographic strata ($\hat{\psi} = 0.911 \pm 0.020$; $\hat{\alpha}[\psi^{11}, \psi^{22}] = 0.0161$, 95% CI = −0.0309 to 0.0631), and recapture rates ($p = 0.097 \pm 0.016$) of banded and radiomarked individuals were not different ($\hat{\alpha}[p_{radioed}, p_{banded}] = 0.145$, 95% CI = −0.510 to 0.800). Combining these data types in a common model resulted in more precise estimates of movement and recapture rates than separate estimation, but ability to detect stratum or mark-specific differences in parameters was weak. We conducted simulation trials to investigate the effects of varying study designs on parameter accuracy and statistical power to detect important differences. Parameter accuracy was high (relative bias [RBIAS] <2%) and confidence interval coverage close to nominal, except for survival estimates of banded birds for the "off study area" stratum, which were negatively biased (RBIAS −7 to −15%) when sample sizes were small (5–10 banded or radioed animals "released" per time interval). To provide adequate data for useful inference from this model, study designs should seek a minimum of 25 animals of each marking type observed (marked or observed via telemetry) in each time period and geographic stratum.

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Wildlife biologists commonly use radiotelemetry to obtain estimates of survival and descriptions of movement (Pollock et al. 1989, White and Garrott 1990) and mark–recapture methods (including both actual captures and resightings of individuals) to estimate population size, survival, and movement patterns (Seber 1982, Pollock et al. 1990). Usually, radiomarked animals are also marked with bands, tags, or other form of identification, and radiomarked animals are often recaptured during the course of the study. Biologists studying several classes of animals have described the simultaneous use of large-scale radiotelemetry and capture–recapture techniques (Garrett and Franklin 1988, Rappole et al. 1989, Griffiths and Christian 1996, Holland et al. 1996), but we are unaware of a single case in which telemetry and mark–recapture data were combined to simultaneously estimate demographic parameters.

A previous model developed by Burnham (1993) allowed estimation of parameters with data from a combined data structure involving live recaptures and recoveries of dead (often, hunter-shot) animals. This model allowed estimation of survival rates as shared parameters

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from both data structures, and separation of mortality from permanent emigration, the latter not provided by standard mark–recapture analysis (Pollock et al. 1990). In this paper we extend this approach to a problem in which mark–recapture data are combined with observations of radiotagged animals. As with combined mark–recapture and recovery analysis (Burnham 1993), there are several advantages to simultaneously using data from both sources. First, precision of survival estimates should be increased by combining 2 sources of information about the same parameter (Burnham 1993). Second, incorporating mark–recapture data into a combined data structure allows for tests of potential radio effects on survival or other parameters (Burger et al. 1991, Pietz et al. 1993, Ward and Flint 1995), enabling unbiased estimation of survival. Third, a combined design allows for separate inference on movement, emigration, and mortality rates that are often confounded in complex ways, particularly in studies at broad spatial scales. For example, survival estimates from traditional open-population, mark–recapture methods are not true survival rates, because mortality and permanent emigration cannot be distinguished (Pollock et al. 1990). If the robust mark–recapture design (Kendall et al. 1997) is used, it is possible to separate emigration and survival. Alternatively, if radiomarked study animals are followed after they leave a study area or local population, it is possible to remove the emigration component from mark–recapture survival estimates by combining both data types in a common model.

In this paper we describe a model structure for estimating survival, movement, and capture rates using mark–recapture and radiotelemetry data. We provide an example using field data on wood thrushes, and we describe how demographic parameters can be estimated with a new version of program MSSURVIV (Brownie et al. 1993). We also use Monte Carlo simulation to evaluate bias, precision, and statistical power under a combined analysis of mark–recapture and radiotelemetry data.

METHODS

Field Study

We captured adult wood thrushes in mist nets at PNWR in central Georgia during the 1996 breeding season. Individuals were initially captured on a study area composed of 7 forest management compartments, each approximately 400 ha in size. Although our study area consisted of 7 mostly non-connected forest compartments, for the purposes of this model the "study area" is considered to be contiguous. We mist netted on the 7 study compartments for 4,275 net-hours, rotating capture effort among compartments at least every 3 weeks. All captured birds were marked with BRD leg bands, and radiomarked birds were equipped with 1.6-g transmitters using thigh harnesses (Rappole and Tipton 1991, Powell et al. 1998). We performed daily searches for radiomarked birds, both on and off the study area. Data were summarized into weekly discrete time intervals for analysis by a Kaplan-Meier type staggered-entry radiotelemetry design (Kaplan and Meier 1958) and a 13-sample Cormack-Jolly-Seber (C-J-S) design (Pollock et al. 1990).

Model Notation and Assumptions

The notation used here follows Brownie et al. (1993) and Pollock et al. (1989, 1990). We expanded the theory of multiple strata mark–recapture models (MSSURVIV, Brownie et al. 1993) to include radiomarked animals. Two geographic strata were allowed: (1) on the study area (the area on which mist netting efforts occurred), and (2) off the study area (an area searched for radio signals but on which no mist-netting was conducted). To avoid confusion, we refer to non-radiomarked individuals as "banded." Also, "recapture" of radiomarked individuals refers to physical captures during netting (or other capture method) efforts, not the "capture" of an individual's radio signal during telemetry observations. Let r denote location, where $r = 1$ denotes that an animal is on the study area, and $r = 2$ denotes that an animal is off the study area at time i; the pair rs denotes locations at time i and $i+1$, respectively. The following statistics are then sufficient for the estimation procedure:

$R_i^{(1)}$ = banded (no transmitter) releases at time i on study area,

$m_{ij}^{(11)}$ = members of $R_i^{(1)}$ that are next caught (on study area) at time j,

$A_i^{(r)}$ = radiomarked releases (or relocations) at time i, area r,

$a^{(r1)}_{i,i+1}$ = member of $A_i^{(r)}$ captured at time $i + 1$ on study area,

$b^{(rs)}_{i,i+1}$ = members of $A_i^{(r)}$ relocated (not caught) at time $i + 1$ on area s,

$d_i^{(r)}$ = members of $A_i^{(r)}$ that die between time i and $i + 1$,

$r = 1, 2, \quad s = 1, 2, \quad i = 1, \ldots, t.$

Parameters to be estimated are:

$\psi_i^{(rs)}$ = probability of banded or radiomarked bird moving from area r to area s between sampling occasion i and $i + 1$, $r = 1, 2, s = 1, 2,$

$S_{Bi}^{(r)}$ = probability of banded-only birds on area r at time i surviving from sampling occasion i to $i + 1$, $r = 1, 2,$

$S_i^{(r)}$ = probability of radiomarked birds on area r at time i surviving from sampling occasion i to $i + 1$, $r = 1, 2,$

$p_{Bi}^{(1)}$ = probability of banded-only birds on area 1 at time i being recaptured at sampling occasion i,

$p_i^{(1)}$ = probability of radiomarked birds on area 1 at time i being recaptured at sampling occasion i (by definition no birds are captured on area 2),

$i = 1, \ldots, t.$

The assumptions of this model include the assumptions of Cormack-Jolly-Seber type mark–recapture models (Seber 1982, Pollock et al. 1990), Kaplan-Meier type survival analysis models (Kaplan and Meier 1958, Pollock et al. 1989), and multiple strata mark–recapture models (Brownie et al. 1993). Additionally, we considered 3 other assumptions to the model.

Assumption 1: Radiomarked and Banded Individuals Behaved Independently with Respect to Capture, Survival, and Movements.—Although we believe that most mated individuals did not affect the survival of their mates or neighbors, this assumption could be violated if a radiomarked member of a mated pair influences the behavior of the banded mate (Schmutz et al. 1995). With only 2 exceptions, both members of all wood thrush pairs in our sample were radiomarked, and in those exceptions the mate was never captured and banded. This assumption may present the largest potential bias to future studies if precautions are not taken to radiomark both members of the pair, but if the second assumption (see below) is not violated, violations of the first assumption should not bias survival, movement, or recapture estimates.

Assumption 2: Radiomarked Individuals Located Off Study Area were not Affected by Earlier Capture Events on the Study Area.—The model was Markovian (Brownie et al. 1993); that is, the model was not structured to provide "memory" of previous capture events during the season. Therefore, birds became part of a new cohort when they switched to a new geographic stratum. This assumption might be violated in cases of extreme habitat effects on physiology that could linger after moving to another area. Powell (1998) found no effect of PNWR forest habitat management on survival of adult wood thrushes, which included birds in our sample.

Assumption 3: Temporary or Permanent Emigration from the Entire 2-patch System was not Possible.—The "off study area" theoretically includes all areas outside of our study area. Unless satellite tracking is used, however, it is possible for animals to emigrate beyond the area that can be logistically searched with aerial telemetry. Therefore, the third assumption may restrict this kind of analysis to certain times of year and sampling situations. Movements out of the 2-patch system are treated as deaths by the mark–recapture component of the model, and survival estimates could be biased by violations of this assumption. To avoid such violations, our sampling period occurred at the time of year before large premigratory and migratory movements.

Model Structure

The underlying statistical model includes 2 components with common survival parameters that serve to link the probability models for the 2 data types: (1) recaptures of banded animals and (2) relocations of radiomarked animals. The inclusion of radiomarked animals allows estimation of movement rates, not possible from recaptures alone. These components are modeled separately, below, and combined in a likelihood for the estimation of all parameters.

Mark–recapture Model for Banded Individuals.—Survival and recapture rates for banded-only individuals can be estimated by extension of Cormack-Jolly-Seber models (Pollock et al.

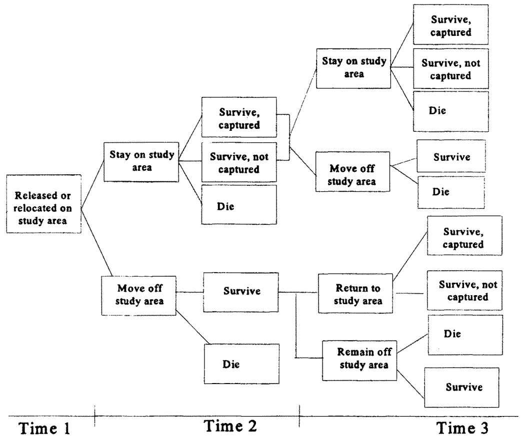

Fig. 1. Possible movement histories on and off study area for banded-only individuals over 3 periods following initial capture.

1990) to allow inter-strata movement. Because animals can move in and out of the study area during each time period, cell likelihoods become increasingly complex as the number of intervals between capture and recapture increase (Fig. 1) and are generally too long for the usual SURVIV input format (Brownie et al. 1993). Therefore, we used an "*m* array" (Burnham et al. 1987) to summarize the data structure and expected values (Table 1). Total releases for period i equal the sum of previously marked (recaptures) and newly captured animals. Thus, after recapture in period i, animals become part of the released cohort for time period $i+1$. These data allow estimation of survival ($S_{Bi}^{(1)}$) and capture ($p_{Bi}^{(1)}$) probabilities for banded birds on the study area (where capture and banding is occurring), but estimation of movement ($\psi_i^{(rs)}$) and off-study area survival rates ($S_i^{(2)}$) require data from radiomarked birds for parameter identification.

Survival and Movement from Telemetry.—Telemetry data allow direct estimation of survival ($S_i^{(r)}$) and movement ($\psi_i^{(rs)}$) parameters for radiomarked birds, both on and off the study area (r = 1, 2). It is also possible to directly estimate the capture probability of radiomarked individuals during each time interval; estimation of this parameter is necessary for inclusion of radiomarked birds in the statistical model, when they become part of a capture–release sample (Table 2).

Radiomarked animals "released" (i.e., captured and released, or not captured but observed by radiotelemetry) at sample occasion i on the study area have 4 possible multinomial outcomes during each time interval: (1) survive, stay on study area, and experience capture in a mist net; (2) survive and stay on study area, but do not experience capture in a mist net; (3) survive and leave study area; and (4) stay on study area and die (Table 2). These outcomes are conditional on birds being observed in the interval (i, $i+1$); therefore individuals right censored due to (radio failure or signal loss) were removed from the cohort ($A_i^{(1)}$). Radiomarked birds located off the study area have 4 possible multinomial outcomes during each time interval: (1) survive, return to study area, and experience capture in a mist net; (2) survive and return to study area, but do not experience capture in a mist net; (3) survive and remain away from the study area; and (4) remain away from study area and die (Table 1). Right-censored individuals are, again, removed from the cohort total ($A_i^{(2)}$).

A global model structure for the combined (banded and radiomarked birds) would allow for variation in survival and capture parameters by time period, stratum, and marking method, and in movement parameters by time period and stratum. Simplified models can be constructed from this global model by means of constraints on these parameters. For example, because mortality events were so rare (Powell 1998), we did not consider a time-specific model, and allowed parameters to vary only by stratum and marking method. We used likelihood–

Table 1. Model expectation structure for estimation of survival (S), movement (ψ), and capture (p) probabilities using data from conventional marking (banding).

Period released	No. released[a]	No. next recaptured in period 2	No. next recaptured in period 3
1	$R_1^{(1)}$	$R_1^{(1)}S_{B1}^{(1)}[1 - \psi_1^{(12)}]p_{B2}^{(1)}$	$R_1^{(1)}S_{B1}^{(1)}p_{B3}^{(1)}\{[1 - \psi_1^{(12)}][1 - \psi_2^{(12)}][1 - p_{B2}^{(1)}]S_{B2}^{(1)} + \psi_1^{(12)}S_{B2}^{(2)}\psi_2^{(21)}\}$
2	$R_2^{(1)}$		$R_2^{(1)}S_{B2}^{(1)}[1 - \psi_2^{(12)}]p_{B3}^{(1)}$

[a] In each time period banded animals are released in stratum 1 ("on study area") and may be recaptured in subsequent periods (e.g., by mist-netting); physical recapture only occurs in stratum 1.

Table 2. Model expectation structure for estimation of survival (S), movement (ψ), and capture (p) probabilities using data from releases of radiomarked animals.

			Fate in next time period			
				Relocated by telemetry		
Period released	Area released	No. released[a]	Recaptured on area	On area	Off area	Died
1	On area	$A_1^{(1)}$	$A_1^{(1)}S_1^{(1)}(1 - \psi_1^{(12)})p_2^{(1)}$	$A_1^{(1)}S_1^{(1)}(1 - \psi_1^{(12)})(1 - p_2^{(1)})$	$A_1^{(1)}S_1^{(1)}\psi_1^{(12)}$	$A_1^{(1)}[1 - S_1^{(1)}]$
	Off area	$A_1^{(2)}$	$A_1^{(2)}S_1^{(2)}\psi_1^{(21)}p_2^{(1)}$	$A_1^{(2)}S_1^{(2)}\psi_1^{(21)}(1 - p_2^{(1)})$	$A_1^{(2)}S_1^{(2)}(1 - \psi_1^{(21)})$	$A_1^{(2)}[1 - S_1^{(2)}]$
2	On area	$A_2^{(1)}$	$A_2^{(1)}S_2^{(1)}(1 - \psi_2^{(12)})p_3^{(1)}$	$A_2^{(1)}S_2^{(1)}(1 - \psi_2^{(12)})(1 - p_3^{(1)})$	$A_2^{(1)}S_2^{(1)}\psi_2^{(12)}$	$A_2^{(1)}[1 - S_2^{(1)}]$
	Off area	$A_2^{(2)}$	$A_2^{(2)}S_2^{(2)}\psi_2^{(21)}1p_3^{(1)}$	$A_2^{(2)}S_2^{(2)}\psi_2^{(21)}(1 - p_3^{(1)})$	$A_2^{(2)}S_2^{(2)}(1 - \psi_2^{(21)})$	$A_2^{(2)}[1 - S_2^{(2)}]$

[a] In each period $A_i^{(r)}$ animals are "released" (i.e., captured, radioed and released, or re-observed via radio signals) in each stratum (r = 1, "on study area"; r = 2, "off study area"). In the next time period (i + 1) these may be captured or re-observed (but not captured) in either stratum. Animals "recaptured" by either method at time i become members of the new release cohort associated at that time period (e.g., a radiomarked bird released in time period 1 in stratum 1 and re-observed in time period 3 in stratum 2, is now a member of $A_3^{(2)}$. See text for definition of model parameters.

ratio tests to test for equal rates of survival and recapture between banded and radiomarked birds, and equal rates of movement and survival between geographic strata. Because of small cohort sizes, we used a corrected Akaike Information Criterion (AIC_c) to choose the best model (Burnham and Anderson 1998).

To compare survival and other parameters between groups we defined

$$\alpha(\theta_1,\theta_2) = \log(\theta_1/\theta_2) \qquad (1),$$

where θ_1,θ_2 are 2 parameters stratified by the groups under comparison. For example, $\alpha(S,S_B) = \log(S/S_B)$ would be expected to equal 0 when survival of birds marked by the 2 methods is identical, and to be negative under adverse survival impacts of telemetry. We estimated α by

$$\hat{\alpha}(\theta_1,\theta_2) = \log(\hat{\theta}_1/\hat{\theta}_2) \qquad (2),$$

where $\hat{\theta}_1,\hat{\theta}_2$ are estimates of the quantities under comparison. Variances for $\hat{\alpha}$ were computed by application of the delta method (Seber 1982: 7) and used to estimate asymptotic normal confidence intervals for α, which provided an estimate of the real effect size and a gauge of the strength of our results (Gerard et al. 1998). To obtain maximum likelihood estimates for the model parameters, J. E. Hines adapted MSSURVIV, a modification of program SURVIV (White 1983) designed for problems with multiple strata, and movement among strata. The new version, MSSRVRT, is similar to MSSURVIV, but it incorporates the combined radiotelemetry and capture–recapture data structure (Tables 1, 2). At present, the program allows 2 geographic strata and 1 age class. The number of time intervals can vary between 3 and 20. The MSSRVRT code can be obtained from J. E. Hines.

Monte Carlo Simulation

The data from our wood thrush example, although typical of such studies, were insufficient to adequately evaluate the statistical performance of our method. To further investigate the properties of the methodology under general circumstances, we conducted a Monte Carlo simulation experiment. First, we specified a general model (H_A) in which survival and movement parameters differed by geographic strata (on or off study area) and the type of marking (banded only vs. radiomarked). We selected parameter values as follows:

$$\psi^{(11)} = 0.88, \qquad \psi^{(22)} = 0.92$$
$$S^{(1)} = 0.93, \qquad S^{(2)} = 0.97$$
$$S_B{}^{(1)} = 0.95, \qquad S_B{}^{(2)} = 0.99,$$

based on a range of values estimated from our model set, and representing differences that we would be interested in detecting in a biological study. For instance, weekly survival rates of 0.95–0.97 for banded vs. 0.93–0.95 for radioed birds would represent a profound survival impact of telemetry when considered over a typical field season (10-week survival of 0.48–0.74 for radioed vs. 0.60–0.90 for banded birds).

We then examined the influence of a range in sample sizes ($R_i^{(1)}$; $A_i^{(r)}$, $i = 1, 2$) and recapture rates ($p_i^{(r)} = p_{Bi}^{(r)} = p$) by establishing combinations of sample sizes (5, 10, and 25 for each marking type) and recapture rates (0.11, i.e., similar to our study; 0.20, and 0.40). For each trial we used PROC SIMULATE in program SURVIV (White 1983) to generate the matrices of data for the model structure identical to that in Tables 1 and 2 (12 recapture periods, 2 geographic strata, marking by banding alone and by radiotelemetry). We estimated RBIAS and mean squared error (RMSE) for the parameters of interest as

$$\text{RBIAS} = \frac{\frac{1}{n}\sum_{i=1}^{n}\hat{\theta}_i - \theta}{\theta} \times 100\%, \qquad (3)$$

and coefficient of variation (CV) as

$$\text{CV} = \frac{\sqrt{\frac{1}{n-1}\sum_{i=1}^{n}(\hat{\theta}_i - \bar{\theta})^2}}{\theta} \times 100\%, \qquad (5)$$

where $\hat{\theta}_i$ is the estimated parameter for the i^{th} simulation replication from SURVIV, θ is the parameter value, $\bar{\theta} = 1/n \; \Sigma_{i=1}^{n} \hat{\theta}_i$, and $n = 10{,}000$ replications per trial. For each replication we obtained the estimated standard error ($\widehat{\text{SE}}(\hat{\theta}_i)$) for each parameter of interest, an estimated 95% confidence interval (CI) as

$$\hat{\theta}_i \pm 1.96 \times \widehat{\text{SE}}(\hat{\theta}_i), \qquad (6)$$

and determined whether the parameter (θ) was included in the interval; the percentage of the 10,000 replications in which coverage occurred was our estimate of CI coverage for comparison to the nominal 95% coverage. Because of concern about performance of asymptotic estimates of SE under small sample conditions, we also evaluated the relative bias of the SE, taking the empirical estimate of standard deviation of the parameter from the simulations as the best estimate of the true SE:

$$\sigma = \sqrt{\frac{1}{n-1}\sum_{i=1}^{n}(\hat{\theta}_i - \bar{\theta})^2}. \qquad (7)$$

We used this quantity to estimate relative bias of SE (RBIAS_{SE}) as

$$\text{RBIAS}_{\text{SE}} = \frac{\frac{1}{n}\sum_{i=1}^{n}\widehat{\text{SE}}(\hat{\theta}_i) - \sigma}{\sigma} \times 100\%, \qquad (8)$$

where $\widehat{\text{SE}}(\hat{\theta}_i)$ is the estimated SE for $\hat{\theta}$ from the ith simulation, and $\bar{\theta} = 1/n \; \Sigma_{i=1}^{n}\hat{\theta}_i$.

We also evaluated statistical power $(1-\beta)$ to detect various parameter differences of interest, by constructing null hypotheses of no difference in selected pairs of parameters. We formed 3 such null hypotheses: H_1:$\psi^{(11)} = \psi^{(22)}$ (fidelity–movement rates equal between geographic strata), H_2:$S^{(1)} = S^{(2)}$; $S_B{}^{(1)} = S_B{}^{(2)}$ (survival rates equal between strata but differing dependent on marking), and H_3:$S^{(1)} = S_B{}^{(1)}$; $S^{(2)} = S_B{}^{(2)}$ (survival rates equal between marking methods but different between strata). We used the likelihood-ratio tests in SURVIV to test each of these hypotheses against the alternative H_A as previously defined, controlling Type I error at $\alpha = 0.05$. We estimated power for each hypothesis test as the proportion of the $n = 10{,}000$ simulation replications in which the test was rejected.

RESULTS

Field Study

We captured 73 adult wood thrushes during the 1996 breeding season of which 45 were banded only and 28 were equipped with radiotransmitters. We recaptured 17 radiomarked and 17 banded birds in mist nets at least once on the study area. Thirteen radiomarked birds left the study area during the study, as determined by aerial telemetry. We continued to follow these birds until radio failure or death occurred; 4 of the 13 emigrated but eventually returned to the study area. Recapture and relocation data for the banded and radiomarked wood thrushes are summarized in Tables 3 and 4, excluding 5 bird right-censored (1 each in weeks 6 and 9, and 3 in week 12); only 2 wood thrushes died during the breeding season in 1996. These data were used to fit 11 models with differing assumptions

Table 3. Recaptures of banded adult wood thrushes at the Piedmont National Wildlife Refuge in Georgia, 1996.

Period released	Number released	Number next recaptured in period 2	3	4	5	6	7	8	9	10	11	12	13
1	5	0	1	0	0	0	0	0	2	0	0	0	0
2	2		1	1	0	0	0	0	0	0	0	0	0
3	6			0	0	1	0	1	0	0	0	0	0
4	7				0	0	0	0	0	0	0	1	0
5	6					1	0	0	0	0	0	1	0
6	7						3	0	0	0	0	0	0
7	8							1	0	0	1	0	0
8	4								0	0	0	0	0
10	3										1	0	0
11	7											1	1
12	6												0

about differences in survival, movement, and capture rates with respect to geographic strata and marking method (Table 5). The model with the lowest AIC assumed no variation in survival, capture, or movement rates (thus, containing 3 parameters: S, ψ, and p), and estimated a weekly survival rate of 0.989 ± 0.007 (SE; Table 6). Survival of radiomarked birds and banded birds was similar: $\hat{\alpha}(S, S_B = 0.0239$, 95% CI = −0.0196 to 0.0674). Survival rates were slightly higher off the study area ($\hat{\alpha}[S^{(1)}, S^{(2)}] = -0.0578$, 95% CI = −0.0756 to −0.04094), with both mortalities occurring on the study area. Fidelity rates ($\hat{\psi} =$ 0.915 ± 0.021) were similar between both study areas ($\hat{\alpha}[\psi^{(11)}, \psi^{(22)}] = 0.0161$, 95% CI = −0.0309 to 0.0631).

The CV of the survival estimate from the combined model was the same as that from the telemetry model and much lower than the mark–recapture model (Table 6). The CV of movement rates was slightly lower using the combined model than the telemetry-only model, and the CV for recapture rates was lower using the combined model than either of the individual models (Table 6).

Simulation Study

Our selection of the simplest model (all parameters constant over strata and between methods) and the wide CI on $\alpha(\theta_1,\theta_2)$ for all comparisons raised concern that estimates from our model based on small samples might not

Table 4. Recaptures and relocations of radiomarked adult wood thrushes at the Piedmont National Wildlife Refuge in Georgia, 1996.

Period released	Area released	Number released	Fate in next time period: Recaptured on area	Relocated by telemetry: On area	Off area	Died
2	On area	6	0	6	0	0
3	On area	10	2	8	0	0
4	On area	16	2	14	0	0
5	On area	18	3	14	1	0
6	On area	17	1	14	1	1
	Off area	1	0	1	0	0
7	On area	21	1	17	3	0
	Off area	1	0	1	0	0
8	On area	19	3	14	2	0
	Off area	3	0	0	3	0
9	On area	18	4	13	1	0
	Off area	4	0	0	4	0
10	On area	20	1	15	3	1
	Off area	5	0	0	5	0
11	On area	16	0	14	2	0
	Off area	8	0	1	7	0
12	On area	12	1	11	0	0
	Off area	9	0	1	8	0

Table 5. Model structure, AIC values[a], and model goodness-of-fit for all models considered for radiomarked and banded wood thrushes in 1996 at the Piedmont National Wildlife Refuge, central Georgia. Model parameters were: *S*, probability of surviving one week; *p*, probability of being recaptured during week; and ψ, weekly movement probability (Models H_A, H_1, H_2, and H_3 were added to the original model set [models 1–7] for the simulations to estimate bias and power [Table 7]).

	Differ by marking method		Differ by geographic strata				Goodness-of-fit		
Model	*S*	*p*	*S*	ψ	AIC_c	Number of parameters	χ^2	df	*P*
1	No	No	No	No	178.3	3	39.427	45	0.7063
2	Yes	No	No	No	179.4	4	42.232	45	0.5899
3	No	No	No	Yes	180.0	4	34.738	44	0.8399
4	No	No	Yes	Yes	181.3	5	34.461	43	0.8204
5	No	Yes	Yes	Yes	182.4	6	34.671	42	0.7816
6	Yes	No	Yes	Yes	183.7	7	34.738	44	0.8399
7	Yes	Yes	Yes	Yes	185.9	8	33.702	40	0.7483
H_A	Yes	No	Yes	Yes	187.9	7	35.116	41	0.7288
H_1	Yes	No	Yes	No	186.9	6	45.446	42	0.3305
H_2	Yes	No	No	Yes	187.7	5	31.642	43	0.8996
H_3	No	No	Yes	Yes	191.5	4	34.906	43	0.8055

[a] AIC values are modified following Burnham and Anderson (1998).

allow useful biological inferences. Our simulation results were generally reassuring, with little bias except for $\hat{S}_B{}^{(2)}$ (RBIAS <2%; Table 5). Bias exceeded 15% in some simulation trials for $\hat{S}_B{}^{(2)}$ (survival of banded birds off the study area). Bias increased with lower banded sample sizes and with increasing capture probabilities (Fig. 2) and was lowest (~5%) at sample sizes of $R_i{}^{(1)} = 25$ and $p \leq 0.2$. As banded and radioed sample sizes increased, CV of estimates decreased (Fig. 3a–d) and was higher for survival rates on versus off the study area (Fig. 3e). We also conducted a few representative simulation trials with large sample sizes ($R_i{}^{(1)} = A_i{}^{(r)} = 10{,}000$); all parameter estimates from these trials were close to unbiased (RBIAS <0.01%), confirming that bias is a small-sample phenomenon. Asymptotic SE of parameter estimates typically overestimated actual SE (σ). Standard error estimates were particularly poor for $SE(\hat{S}^{(2)})$, especially at low sample sizes ($R_i{}^{(1)} = 5$, $A_i{}^{(r)} = 5$; $RBIAS_{SE} = 549\%$); bias was reduced at higher sample sizes but still was positive ($R_i{}^{(1)} = 25$, $A_i{}^{(r)} = 25$; $RBIAS_{SE} = 43.7\%$). The small values of RBIAS and positive bias in standard error estimates produced CI coverages at or above the nominal value of 0.95 (Table 7).

Power to detect specific parameter differences was generally low, averaging 0.324 for H_1 (range 0.165–0.548), 0.485 for H_2 (range 0.200–0.825), and 0.076 for H_3 (range 0.041–0.153). We examined the relationship between power and sample size for $p = 0.11$ (capture rates slightly higher than in our study; Fig. 4). Tests for stratum-specific (H_2 vs. H_A) survival approached reasonable power (0.8) at the upper ranges of sample sizes considered (25 banded animals released and 25 animals sighted and "released" in each area, during each time period). Tests for stratum-specific movement (H_1 vs. H_A) and mark-specific survival (H_3 vs. H_A) had power <0.6 for all of the combinations of sample size considered. Power for all tests was sensitive to radio sample sizes but relatively insensitive to banded sample sizes (Fig. 4).

DISCUSSION

The combined model allowed for a direct hypothesis test for differences in survival between

Table 6. Weekly probabilities and standard errors estimated for male and female wood thrushes in 1996 at the Piedmont National Wildlife Refuge by best fitting (A) combined mark-recapture and telemetry model, (B) mark-recapture model, and (C) telemetry model. Parameters estimated are: *S*, survival of individuals; ψ, probability of staying on the study area or off the study area (complement of moving to a new area); and *p*, recapture of individuals on the study area.

	A—Combined model			B—Mark-recapture model			C—Telemetry model		
Parameter	Estimate	SE	% CV	Estimate	SE	% CV	Estimate	SE	% CV
S	0.989	0.007	0.71	1.000	0.109	10.90	0.990	0.007	0.71
ψ	0.910	0.020	2.20	—[a]	—[a]	—[a]	0.837	0.026	3.11
p	0.097	0.016	16.49	0.205	0.065	31.71	0.111	0.027	24.3

[a] Parameter cannot be estimated with this model structure.

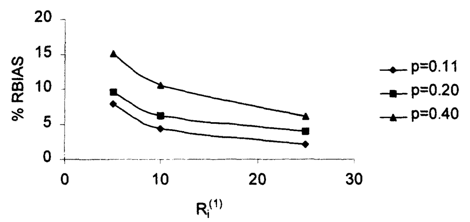

Fig. 2. Relative bias of estimates of survival rates for banded birds off study area ($S_B^{(2)}$) as a function of weekly banded sample size ($R_i^{(1)}$ = 5, 10, 25) and capture probabilities (p = 0.11, 0.20, 0.40) averaged across all values of radio sample size ($A_i^{(r)}$ = 5, 10, 25, r = 1,2).

banded and radiomarked animals. Our data did not suggest that the radiotransmitter affected survival of radiomarked wood thrushes during the breeding season. However, the mark–recapture data was sparse. Confidence interval widths on survival and movement log ratios showed that both negative and positive effects easily could have gone undetected. However, earlier research at the same study location also provided no evidence that radiomarking affected between-year return rates of wood thrushes banded during 1993–95 (Powell et al. 1998).

Although the combined model has the potential to decrease the variability in survival rates, combining our mark–recapture and telemetry data did not result in greater precision for survival estimates than the telemetry-alone model (Table 6) because most of the information about mortality comes from observed deaths of raditagged birds. Precision of recapture and movement rates did increase under the combined model. Our mark–recapture sample was not large, and the benefits of combining data should increase as more data from each source is available.

We were able to estimate the weekly fidelity rate to our study area ($\psi^{(11)}$), and its complement ($\psi^{(12)}$), the probability of emigration from the study area. Emigration rates are needed to parameterize spatially-based population models (Conroy et al. 1995, Noon and Sauer 1992). Our study design was not originally designed to measure immigration into the study area ($\psi^{(21)}$), although 4 radiomarked birds moved back onto the study area after leaving. Biologists should consider initially marking animals off the study area to improve estimates of immigration to the study area and to generate more powerful hypothesis tests about movement rates. Our results suggest that a landscape perspective is critical to managing songbird populations at

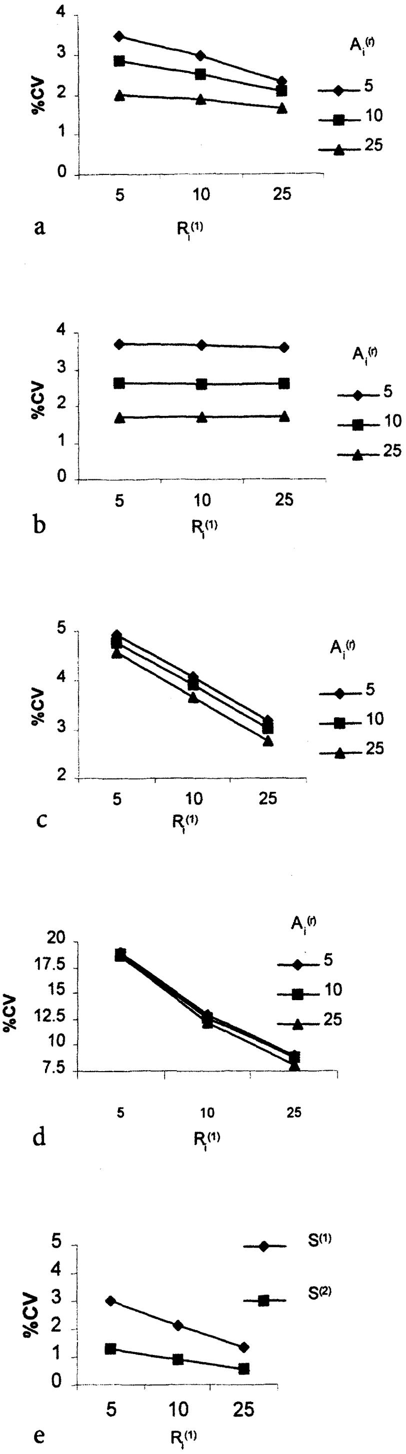

Fig. 3. Coefficient of variation (CV) of estimates of fidelity rates to study area (a, $\psi^{(11)}$) and off study areas (b, $\psi^{(22)}$), and survival rates of banded birds on (c, $S_B^{(1)}$) and off (d, $S_B^{(2)}$) as a function of banded sample size ($R_i^{(1)}$ = 5, 10, 25) and of radio sample size ($A_i^{(r)}$ = 5, 10 25, r = 1,2). (e) CV of estimates of survival rates of radioed birds on ($S^{(1)}$) and off ($S^{(2)}$) study area as function of radio sample size ($A_i^{(r)}$ = 5, 10, 25, r = 1,2). Capture probabilities for all simulations equal (p = 0.2).

Table 7. Results of 27 simulation trials (n = 10,000 each) examining relative bias (RBIAS), relative mean squared error (RMSE), relative bias of estimated standard error ($RBIAS_{SE}$), and coverage of 95% confidence intervals for selected parameters in Model H_A (Table 5) under a range in number of banded ($R_i^{(1)}$) and radiomarked ($A_i^{(r)}$; i = 1,2) animals released (5, 10, and 25) and probabilities of recapture (0.11, 0.20, and 0.40) in each time period (e.g., 1-week periods). Parameters estimated included: $\psi^{(11)}$ and $\psi^{(22)}$, the weekly probability of staying in area 1 or area 2; $S_B^{(1)}$ and $S_B^{(2)}$, the weekly survival of banded-only birds on area 1 and area 2; $S^{(1)}$ and $S^{(2)}$, the weekly survival of radiomarked birds on area 1 or area 2; and p, the weekly probability of being recaptured.

Parameter	% RBIAS $\bar{x}$	% RBIAS Range	% RMSE $\bar{x}$	% RMSE Range	% CV $\bar{x}$	% CV Range	% $RBIAS_{SE}$ $\bar{x}$	% $RBIAS_{SE}$ Range	% CI coverage $\bar{x}$	% CI coverage Range
$\psi^{(11)}$	−0.26	−0.74 2.08	2.46	1.59 3.80	2.37	1.37 3.75	11.12	2.35 20.95	96.95	95.29 98.41
$\psi^{(22)}$	−0.20	−3.86 0.43	2.75	1.69 4.40	2.55	1.31 3.75	2.84	−1.23 19.43	91.84	89.41 93.99
$S_B(1)$	0.96	0.72 1.62	4.10	2.27 6.37	3.95	2.15 6.28	40.26	25.74 62.72	99.50	97.44 99.97
$S_B^{(2)}$	−7.28	−15.13 0.62	16.63	5.34 29.70	14.87	5.30 15.58	47.98	31.08 116.05	99.68	98.46 100.00
$S^{(1)}$	−0.01	−0.03 0.00	2.15	1.33 3.01	2.15	1.33 3.01	2.13	−3.08 11.51	90.13	84.01 93.83
$S^{(2)}$	0.01	−0.01 0.02	0.93	0.58 1.30	0.93	0.58 1.30	274.52	40.62 549.38	93.46	84.34 99.11
p	0.00	−1.11 2.98	11.58	4.90 23.21	11.53	4.88 23.21	6.21	−0.56 12.68	95.97	95.18 96.92

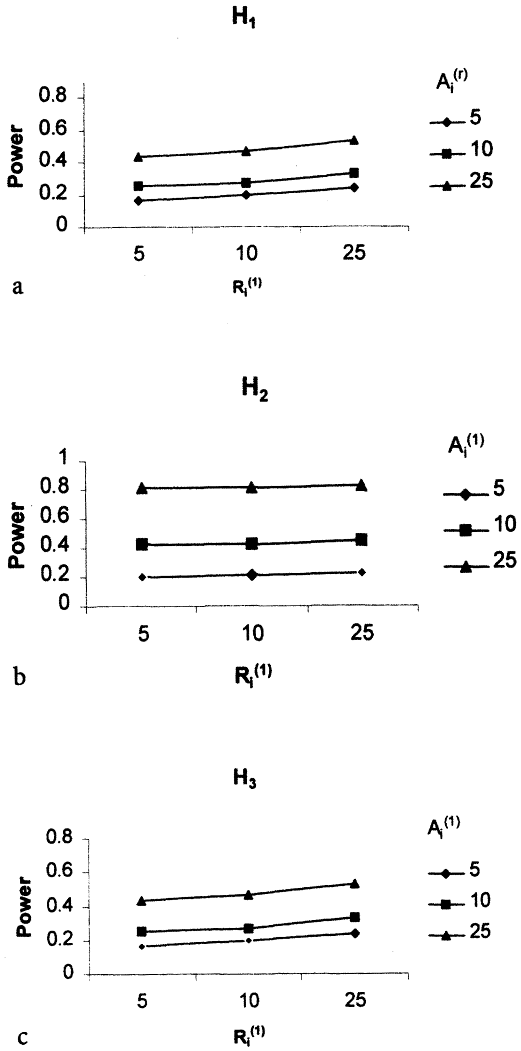

Fig. 4. Power to test H_1:$\psi^{(11)} = \psi^{(22)}$ (fidelity–movement rates equal between geographic strata), H_2:$S^{(1)} = S^{(2)}$; $S_B^{(1)} = S_B^{(2)}$ (survival rates equal between strata but differing dependent on marking), and H_3:$S^{(1)} = S_B^{(1)}$; $S^{(2)} = S_B^{(2)}$ (survival rates equal between marking methods) for p = 0.11, as a function of weekly banded and radioed sample sizes ($R_i^{(1)}$, $A_i^{(r)}$, r = 1,2) releases.

PNWR because nearly 10% of our sample emigrated from the study area each week. Wood thrushes at PNWR appear to use large geographic areas during the breeding season, including public and private lands surrounding PNWR (Powell 1998).

The bias in $\hat{S}_B^{(2)}$ for sample sizes similar to ours raises concerns about the interpretation of parameter estimates. We note that this parameter appears in the model structure (Tables 1, 2) only when birds are not recaptured in the first sampling period after release (i + 1) but in a subsequent period (e.g., $i + 2$) and that the frequency of these events will decrease as capture probabilities (p_{Bi+1}) increase; this may explain the increasing bias in $\hat{S}_B^{(2)}$ with increasing capture rates (Fig. 2). Again, this bias diminishes rapidly as banded sample sizes increase; at small sample sizes, model selection criteria (Burnham and Anderson 1998) should usually result in the combined estimation of survival across marking methods, as evidenced by the lower power of the tests to reject H_3 (Fig. 4). In order to provide adequate power to detect meaningful effects, and keep bias reasonably low, we recommend that future studies seek to obtain a minimum of 25 animals of each marking type observed (by capture or telemetry) in each time period. Of course researchers will have little control over how many animals actually occur in each stratum because of random, inter-stratum movements. Sampling effort must be sufficient to assure a reasonable probability of capture (e.g., $p > 0.20$) in the study area (i.e., region where animals are subject to capture) and virtually certain detection of radiomarked animals over appropriate time intervals (e.g., 1-week periods, as in this study). If these criteria cannot be met, researchers should consider pooling adjacent time periods to increase sample sizes. When these efforts still result in inadequate sample sizes, or require pooling over long intervals (i.e., over which C-J-S assumptions of "instantaneous release" are likely violated), we recommend using separate modeling and analysis of each marking type by C-J-S, Kaplan-Meier, and other methods.

We caution that our wood thrush example may not be fully illustrative of the potential for this or similar study designs to address ecological questions. Our "study area" and "off study area" strata were similar with respect to habitat quality, whereas in many studies (e.g., those directed at comparisons of habitats managed differently) areas might be expected to differ *a priori* with respect to survival or other demographic parameters. Designs directed at detecting habitat-specific survival should be especially attentive to assuring that sample sizes provide adequate statistical power for detecting important differences. Our simulation studies emphasize the importance of adequate sample sizes to allow reliable parameter estimation and examination of spatial and other sources of variations. Designs in which some recapture efforts are made in all strata (corresponding to $p_i^{(2)} > 0$ in our wood thrush example) may be more appropriate for addressing such questions, and estimates for this slightly more general model can also be obtained from MSSRVRT. Such designs are a natural extension of spatially-stratified C-J-S models (Brownie et al. 1993) to allow for simultaneous analysis of both mark–recapture and telemetry data.

Demographic analyses may be more complete and, in some cases, more precise after using the combined model than by using either the telemetry model or mark–recapture models alone. Standard C-J-S models do not allow separation of movement and survival parameters for banded birds. Movement parameters are estimable with radiotelemetry data alone, but we were able to increase the precision of the movement parameters by adding movement information from banding data. Under appropriate study designs (i.e., adequate sample sizes, particularly of radiomarked birds) tests for differences in survival rates between banded birds and radiomarked birds can be conducted. Despite the usefulness of the models presented, biologists must understand and consider the life history of their study species when using this method to estimate demographic parameters. This model structure requires careful planning of the experimental design, and the field methods are logistically challenging. More complicated models are necessary if assumptions regarding permanent emigration from the entire 2-patch system are violated. However, these models can provide important information to help manage populations at the landscape level.

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